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# Small herbivores slow down species loss up to 22 years but only at early successional stage

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## Abstract

1. The long-term influence of persistent small herbivores on successional plant community configuration is rarely studied. We used a herbivore exclusion experiment along the successional gradient in a salt-marsh system, to investigate the effects of hares and geese, and hares alone, on plant diversity at five successional stages (the earliest, two early, the intermediate and the late successional stages) in the short and long term, i.e. 7 and 22 years, respectively.
2. Plant diversity declined over time at all successional stages except for the earliest one. Small herbivores slowed down species decline, but only at one early successional stage.
3. Small herbivores slowed down species decline via decreasing dominance of preferred grass *Festuca rubra* in the short term, and less preferred *Elytrigia atherica* in the long term. The effects of hares and geese were more pronounced than hares alone, indicating an important additive role of geese, especially in the long term.
4. *Synthesis*. Small herbivores can have a strong and long-lasting impact on plant diversity, but it highly depends on the abundance of small herbivores, which in turn depends on the quality and abundance of forage plants. A diverse herbivore community may have more positive effects on regulating plant communities.

KEYWORDS

dominance, geese, hares, herbivory, plant–herbivore interaction, species richness, succession

## 1 | INTRODUCTION

Small vertebrate herbivores (1 kg < body mass < 10 kg) affect plant community composition and structure (Allan & Crawley, 2011; Crawley, 1990; Johnson et al., 2011; Kuijper & Bakker, 2005; Madsen et al,. 2011; Pascual, Alberti, Daleo, & Iribarne, 2017). Limited studies also suggest that small herbivores impact plant diversity (Alberti, Canepuccia, Pascual, Pérez, & Iribame, 2011; Bakker, Ritchie, Olff, Milchunas, & Knops, 2006; Bromberg, Crain, & Bertness, 2009; Gough & Grace, 1998a, 1998b; Pascual et al., 2017). However, those studies were relatively short-term (<7 years), few studies have been long term (>20 years), and no studies have looked at the effects of small herbivores on plant diversity along successional gradients.

The effects of small herbivores on plant diversity may change along successional gradients. Small herbivores are usually selective grazers (Olff & Ritchie, 1998), and thus, changes in the identity of forage plants during vegetation succession may change the abundance of herbivores, particularly in systems where predators are rare (Schrama, Kuijper, Veeneklaas, & Bakker, 2015). The abundance of herbivores is sometimes, if not always, more important than herbivore

size in regulating plant communities (Olofsson, Hulme, Oksanen, & Suominen, 2004). For instance, in a salt-marsh system, vegetation succession leads to taller and more dense plants, an increase in C:N ratio, and litter accumulation at later successional stages. This process reduces forage quality, which in turn reduces the abundance of herbivores, and ultimately their impacts on vegetation at later successional stages (Van de Koppel, Huisman, Wal, & Olff, 1996; Olff, Leeuw, Bakker, Platerink, & Wijnen, 1997). In addition, effects of small herbivores on plant diversity depend on the dominance of forage plants: herbivores decrease plant diversity when dominance is low, while they increase plant diversity when dominance is high (Hillebrand et al., 2007; Koerner et al., 2018). However, how changes in both quality and dominance of forage plants along the successional gradient would modify herbivore effects remains unclear.

Vegetation succession usually takes a long time to develop, therefore, long-term herbivore exclusion experiments using permanent plots are essential to fully assess the effects of small herbivores on plant diversity (Olff & Ritchie, 1998). In addition, chronosequences (space-for-time substitutions) also provide another good way to evaluate long-term effects (Foster & Tilman, 2000). We therefore combine these two approaches by using the salt-marsh system on the barrier island of Schiermonnikoog as a case study. A natural successional gradient is present here (Olff et al., 1997): early successional stages are dominated by *Puccinellia maritima* and *Festuca rubra*, preferred by hares and geese, while late successional stages are dominated by *Elytrigia atherica* (Olff et al., 1997; Van Der Wal, Egas, Veen, & Bakker, 2000; Van Der Wal, Kunst, & Drent, 1998), less preferred by hares and geese (Fokkema et al., 2016; Kuijper, Nijhoff, & Bakker, 2004). Previous work from this saltmarsh indicates that hares, and to a lesser extent, geese, affect plant composition, particularly at early successional stages (Kuijper & Bakker, 2005). However, the hare population has declined by more than 50% in the last two decades (Schrama et al., 2015), while geese populations remain stable (Figure S1).

A small-herbivore exclusion experiment was initiated in 1994 at five successional stages to investigate the effects of small herbivores (hares and geese, hares alone) on plant diversity. In addition, we compared the short (7 years) and long-term (22 years) effects of small herbivores along this successional gradient. Taken together, we evaluated long-term effects of small herbivores using two approaches, one is using successional stages (space-for-time), and the other using change in permanent plots from 1995 to 2016. We predicted that the effects of small herbivores would only be apparent at early successional stages, as less preferred plants become dominant at late successional stages. In addition, these effects would only be apparent in the short term at early stages, as vegetation succession leads to less preferred plant species in the long term.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The experiment was conducted in the back-barrier saltmarsh of the island of Schiermonnikoog (53°30′N, 6°10′E), the Netherlands. The eastern part of the saltmarsh (the study area) is only grazed by small herbivores, including spring staging Brent Geese (*Branta bernicla*), Barnacle Geese (*Branta leucopsis*), and year-round present Brown hares (*Lepus europaeus*) and rabbits (*Oryctolagus cunniculus*). Hares and geese are the most important herbivores, while predators are rare in this system (Van De Koppel et al., 1996; Kuijper & Bakker, 2005; Schrama et al., 2015; Wal, Egas, et al., 2000; Van Der Wal et al., 1998). A natural successional gradient is present here, as the island expands naturally eastward (Olff et al., 1997): the eastern part of the island is younger than the western part, and different successional stages occur adjacent to one another, naturally separated by creeks (Figure S2). We used a herbivore exclusion experiment initiated in 1994 at five different successional stages. For clarity, we refer to these stages by their ages at the start of the experiment, which were 1, 10, 20, 40, 90 years, respectively. These ages were counted from the year vegetation established at that stage to the year (1994) we started the experiment (Olff et al., 1997). To facilitate later discussion, we also refer stage 1 to the earliest successional stage, 10 and 20 as the early successional stages, 40 as the intermediate successional stage, and 90 as the late successional stage. Characteristics of each successional stage can be found in Table S1.

Here, we focus on the effects of small herbivores on plant diversity in the low marsh (0.43 m + MHT, Mean High Tide). In the low saltmarsh, *P. maritima* and *Suaeda maritima* dominate the earliest successional stage, which are replaced by *F. rubra*, *Artemisia maritima* and *Limonium vulgare* at early successional stages, while *E. atherica* and *Atriplex portulacoides* dominate the intermediate and late successional stages (Olff et al., 1997) (A full list of species can be found in Table S2). *P. maritima* and *F. rubra* are highly preferred by hares and geese, while *A. maritima*, and *E. atherica* are generally not preferred (Kuijper, Beek, Wieren, & Bakker, 2008; Van Der Wal, Wijnen, Wieren, Beucher, & Bos, 2000). Several other plant species such as *Plantago maritima*, *Juncus gerardii*, *Triglochin maritima*, *A. portulacoides* are also grazed by hares and geese (Fokkema et al., 2016; Van Der Wal et al., 1998; Wal, Wijnen, et al., 2000).

### 2.2 | Experimental design

Effects of small herbivores were assessed by comparing three treatments, including (a) ungrazed, i.e. hares and goose exclosures; (b) grazing by hares alone, i.e. goose exclosures; (c) grazing by hares and geese, i.e. non-manipulated. Hare and goose exclosures (at least 7 × 7 m) were constructed with chicken mesh (mesh width 25 mm), extending 1 m above soil level supported by wooden posts every 3.5 m and ropes suspended on top. Goose exclosures (ca. 7 × 7 m) had two metal strands running 0.2 and 0.5 m above ground supported by wooden posts every 3.5 m, and ropes suspended on top. Hares and geese had free access to the non-manipulated areas. Exclosures were effective in preventing the entry of the target herbivores (Kuijper & Bakker, 2005), while smaller animals had free access to all grazing treatments. Smaller

vertebrate herbivores such as rodents (voles and mice) were only rarely observed in this study area. We define hares and geese as the small herbivores, to distinguish them from cattle present in the western part of this system. We nested the three grazing treatments into one block, with two blocks per successional stage (Figure S2). For each grazing treatment, four permanent plots of 2 × 2 m were marked, with a minimum distance of 0.5 m between individual permanent plots. We acknowledge that the limited number of true replicates of our experimental design could hinder the interpretation of the results. Nonetheless, the size and spatial segregation of our grazing treatments, along with the duration of the experiment make our data valuable and unique to evaluate the long-term influence of persistent small herbivores on successional plant community dynamics.

We recorded plant species occurrence and abundance in the permanent plots from June 1995, and continued by yearly recording till July 2001 (see Kuijper & Bakker, 2005). We revisited these exclosures and repeated our measurements in August 2016. We evaluated the abundance (cover) of each plant species using the decimal scale of Londo (1976). To characterize permanent plots at each successional stage biotically and abiotically, we measured clay thickness using a 2 cm Ø soil corer ($n$ = 4 per permanent plot) as a proxy for soil total nitrogen (Olff et al., 1997) in 2001 and 2016. Vegetation height was measured by dropping a Styrofoam disc (19 cm Ø, 20 g) along a calibrated stick to the vegetation ($n$ = 4 per permanent plot) in 2016. Elevation was measured using dGPS (Trimble TSC3) adjacent to the permanent plots in August 2016 ($n$ = 1 per permanent plot). Results of clay thickness, vegetation height and elevation for each grazing treatment at each successional stage are shown in Table S1.

### 2.3 | Droppings

Number of droppings is a good indicator of relative grazing pressure (Kuijper & Bakker, 2005; Van Der Wal et al., 1998; Wal, Wijnen, et al., 2000). To count droppings from hares and geese, we set up a line transect adjacent to the exclosures at each successional stage in 2000 and 2016. Each line transect consisted of 20 plots (4 $m^2$), with at least 10 m distance between each other (Figure S2) (Note that exact position of line transects and plots therein might differ between 2000 and 2016, details also in Kuijper and Bakker (2005)). We counted and removed droppings from hares and geese within plots every two or three weeks for the whole year both in 2000 (October 1999 to September 2000) and 2016 (May 2016 to April 2017).

## 3 | DATA ANALYSIS

### 3.1 | Grazing pressure (droppings)

To compare the grazing pressure from hares and geese from different successional stages in 2000 and 2016, we fitted generalized linear models (glm) with family of quasi-poisson, to account for overdispersion, for hare and goose droppings (the summed whole year droppings for each plot), separately. In the model we used number of hare (goose) droppings as a response variable, and successional stage, year and their interaction as fixed variables. Significance of fixed variables was assessed by removing them from the models and comparing the models using function ANOVA with $F$ test.

### 3.2 | Change in plant diversity

To compare the changes in plant diversity in different grazing treatments along the successional gradient in the short and long term, we fitted linear mixed effect models (lmer) from package lme4 (Bates, Mächler, Bolker, & Walker, 2015) and lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). In the model, change in plant diversity was the response variable, and grazing, successional stage, year, and their interactions were the fixed variables. Random variable was specified as (1| Successional stage: Block) + (1| Successional stage: Block: Grazing) + (1| Successional stage: Block: Grazing: Permanent plot). Year and successional stage were treated as categorical variables. We also fitted another model, where the successional stage was treated as the continuous variable, results can be found in Figure S3 and Table S3. We presented results using the successional stage as a categorical variable in the main text because using it as the continuous variable would require a more careful calibration of those ages, and more ages would be needed. Change in plant diversity (counted as number of species) in each permanent plot was calculated as plant diversity in 2001 or 2016-plant diversity in 1995.

### 3.3 | Species gain and loss

According to Olff and Ritchie (1998), grazing affects plant diversity via species gain (colonization) and species loss (extinction). Therefore, we partitioned change in plant diversity into species gain and loss using package codyn (Hallett et al., 2016). Species gains (or losses) were calculated as number of species gained (or lost) in 2001 or 2016/total number of species observed in both timepoints (i.e. 1995 and 2001 or 2016). We used the same model structure (lmer) as for change in plant diversity, but with species gain and loss as the response variables, respectively.

### 3.4 | Change in percent cover of *F. rubra* and *E. atherica*

We compared the changes in percent cover of *F. rubra* and *E. atherica*. *P. maritima* did not occur as a common species at most successional stages, therefore it was not included in the main text. Changes in abundance of all common species at five successional stages can be found in Figure S5. We refer to species as "common" when their cover exceeds 20% in any permanent plot in any year, i.e. 1995, 2001, 2016. Change in percent cover in each permanent plot was calculated as percent cover in 2001 or 2016 - percent cover in 1995.

We fitted the same model structure (lmer) described above, but with changes in percent cover of *F. rubra* and *E. atherica* as the response variables.

### 3.5 | Relationship between dominance and plant diversity

As several studies suggest that herbivores increase plant diversity via reducing dominance (e.g., Koerner et al., 2018; Mortensen et al., 2017), we explored the relationship between plant diversity and dominance across all successional stages in 1995, 2001 and 2016, separately. We fitted a generalized additive mixed model using package gamm4 (Wood & Scheipl, 2017), where we used plant diversity as the response variable, and grazing, year and their interaction as fixed variables. Smoothers against dominance were fitted for each combination of grazing and year. Random variable was specified as 1| Successional stage /Block/ Grazing/ Permanent plot. We used Berger-Parker dominance index, the proportional abundance of the most abundant plant species. We also used another measure of dominance: 1- evenness; evenness was calculated as H/ ln (S), where H is Shannon's diversity index, and S is species richness. Dominance calculated as 1- evenness takes the abundance of all species into account. We included bare ground in this analysis, as bare ground covered 80%–100% in all permanent plots at stage 1 in 1995. Bare ground in the saltmarsh is often covered by microbial mats, which can reduce the establishment of plants. Therefore, bare ground is not an inert space unoccupied by plants, it has an ecological function and can actively contribute to the dynamics of plant communities. We present the result using Berger-Parker dominance index in the main text. Result using dominance as 1- evenness is similar, and is presented in Figure S6. In addition, results using both indices but without taking bare ground into account are presented in Figure S7.

For models fitted using the lmer function from the package lmerTest, significance of fixed terms was assessed using the function ANOVA (type III), where degrees of freedom were calculated by Satterthwaite's approximation. Models were simplified using the step function, residual plots of final models were visually checked for homogeneity of variance and normality. We tested the contrasts in change in plant diversity, species gain, species loss, percent cover of *F. rubra* and *E. atherica* when grazing or any interaction of grazing with successional stage and year was significant, using function *lsmeans* (Tukey adjust) from package emmeans (Lenth, 2019). We restricted contrasts between grazing treatments within year within successional stage to keep it consistent, as the interaction of grazing, successional stage and year was significant in some models (Table S4). Data analysis was performed in R 3.5.1 (R Core Team, 2018).

## 4 | RESULTS

### 4.1 | Grazing pressure (droppings)

Successional stage and year significantly affected hare and goose droppings (hare, successional stage × year: $F_{4, 195}$ = 6.98, $p$ < .001; goose, successional stage × year: $F_{4, 195}$ = 10.79, $p$ < .001). Stage 10 and 20 had the higher numbers of hare droppings both in 2000 and 2016, stage 20 showed the highest number in 2000, while stage 10 showed the highest number in 2016 (Figure 1). Similarly, stage 1, 10 and 20 had the highest numbers of goose droppings in 2000, while these numbers were lower in 2016 (Figure 1).

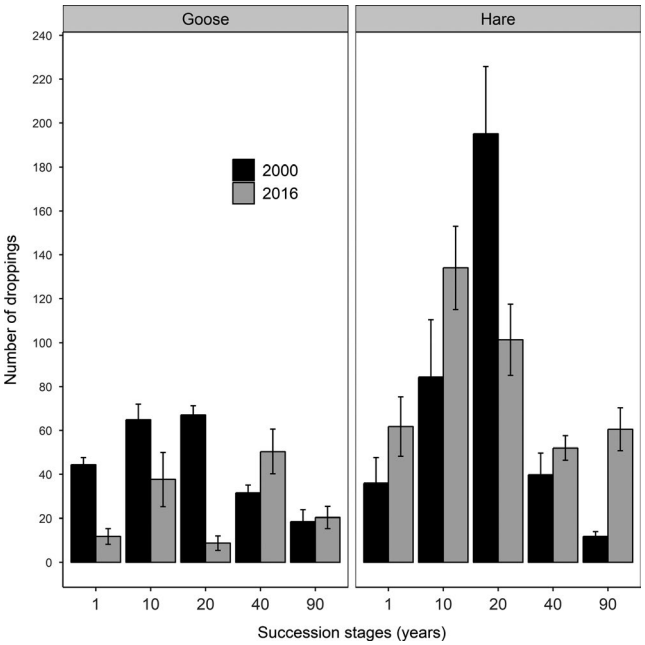


**FIGURE 1** Hare and goose droppings at different successional stages in 2000 and 2016. Droppings were the means (± 1 *SE*) of the 20 plots, each with summed whole year droppings, at each successional stage

### 4.2 | Change in plant diversity

Overall, plant diversity declined in 2001 and 2016 at all successional stages (although it increased at the earliest succession stage) (Figure 2). Small herbivores significantly affected change in plant diversity but only at stage 10 (grazing × successional stage × year: $F$ = 2.31, $p$ = .0255; Table S4). Compared with the ungrazed treatment, hares and geese, and hares alone significantly slowed down species decline at stage 10 in 2001. However, in 2016, only hares and geese together significantly slowed down species decline (Figure 2). Small herbivores slowed down species decline via decreasing species loss (grazing × successional stage: $F$ = 3.5, $p$ = .0338), but not via changing species gain (Figure 3; Table S4).

### 4.3 | Change in percent cover of *F. rubra* and *E. atherica*

Compared with the ungrazed plots, hares and geese significantly suppressed the expansion of *F. rubra* at stage 10 in 2001. However, in 2016, hares and geese significantly increased the abundance of *F. rubra* at stage 10 and 20. In addition, they also significantly increased

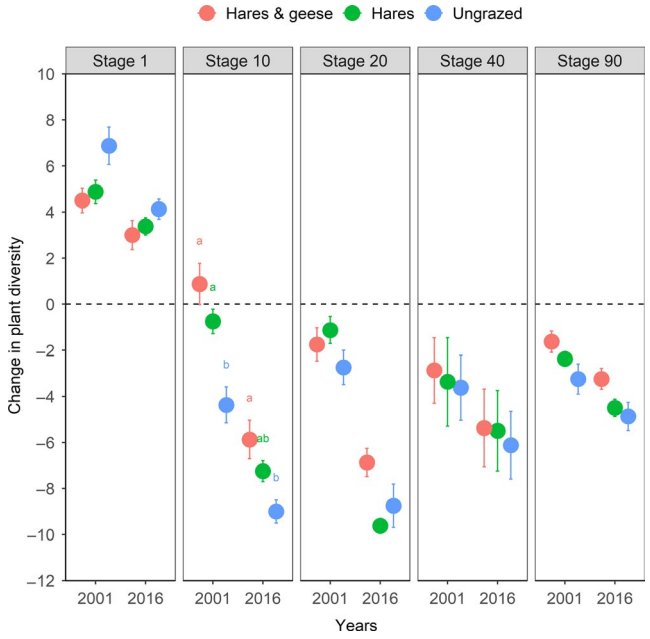


**FIGURE 2** Change in plant diversity in different grazing treatments at different successional stages in 2001 and 2016. Change in plant diversity was calculated as plant diversity in 2001 or 2016 - plant diversity in 1995. Dots are means of each grazing treatment, error bars show ± 1 *SE*. Different letters represent significant differences among grazing treatments for a given year and successional stage at $p < .05$

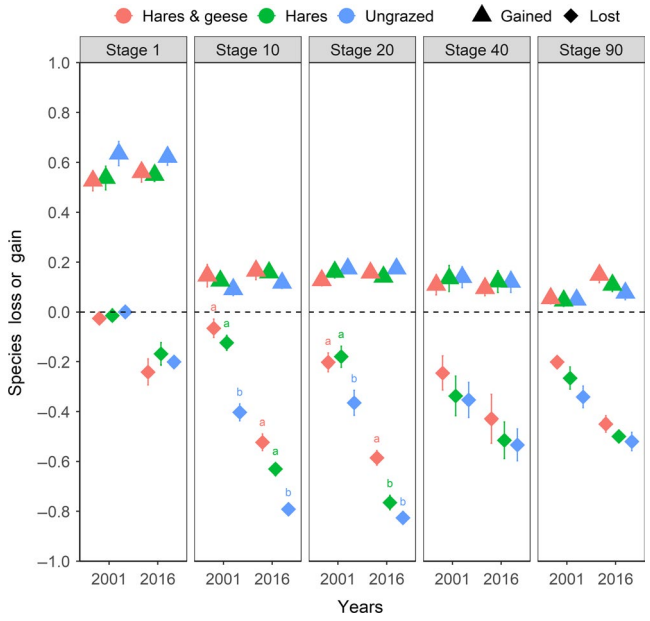


**FIGURE 3** Species gain and loss in different grazing treatments at different successional stages in 2001 and 2016. Species gain or loss was calculated as number of species gained (lost) in 2001 or 2016 / total number of species observed in both timepoints (i.e. 1995 and 2001 or 2016). Dots are means of each grazing treatment, error bars show ± 1 *SE*. Different letters represent significant differences among treatments for a given year and successional stage at $p < .05$


**FIGURE 4** Change in percent cover of *Festuca rubra* and *Elytrigia atherica* in different grazing treatments at different successional stages in 2001 and 2016. Change in percent cover was calculated as percent cover in 2001 (2016) - percent cover in 1995. Dots are means of each grazing treatment, error bars show ± 1 *SE*. Different letters represent significant differences among treatments for a given year and successional stage at $p < .05$

the abundance of *F. rubra*, compared with hares alone, at stage 1 and 10 in 2016 (grazing × successional stage × year; $F = 10.08$, $p < .0001$; Figure 4; Table S4). Compared with the ungrazed, hares and geese suppressed the expansion of *E. atherica* at stage 40 and 90 in 2001. In 2016, they suppressed *E. atherica* at all successional stages (except stage 1). In addition, hares and geese also significantly suppressed *E. atherica* compared with hares alone at stage 10, 40 and 90 in 2016 (grazing × successional stage × year: $F = 8.48$, $p < .0001$; Figure 4; Table S4).

### 4.4 | Relationship between dominance and plant diversity

In 1995, plant diversity declined as the dominance increased regardless of grazing treatments, but only when the dominance exceeded 50%. In 2001, plant diversity declined when dominance increased in ungrazed treatment, but not in hares and geese, and hares alone treatments. In 2016, plant diversity decreased as long as the dominance increased, regardless of grazing treatment. This decline speeded up in ungrazed treatment when the dominance exceeded 50% (Figure 5; Table S3).

## 5 | DISCUSSION

Our 22-year herbivore exclusion experiment along the successional gradient revealed that small herbivores slowed down plant diversity decline, but only at one early successional stage (stage 10), where

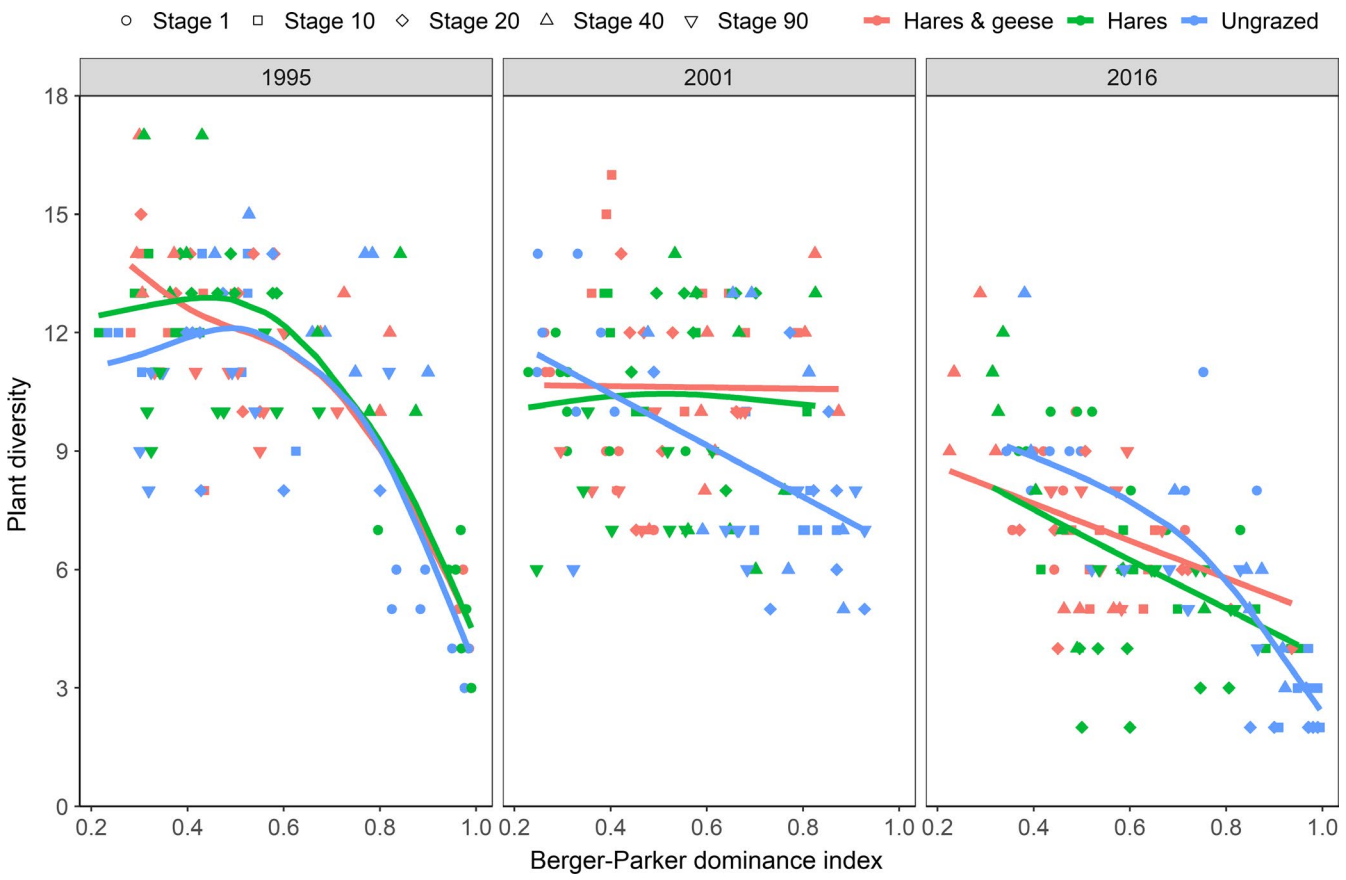


**FIGURE 5** Relationship between dominance and plant diversity across the successional stages in 1995, 2001 and 2016. Lines were fitted with the generalized additive mixed model (Table S3)

we also found more droppings of hares and geese. Small herbivores slowed down species decline via decreasing species loss, which can be attributed to reduced dominance. Small herbivores reduced the dominance of preferred grass *F. rubra* in the short term, and of the less preferred *E. atherica* in the long term. In addition, hares and geese tended to have stronger effects than hares alone, and these effects became more pronounced in the long term. Our results highlight the importance of long-term exclusion experiments along the successional gradient in assessing the effects of small herbivores on plant diversity.

As we hypothesized, small herbivores have pronounced effects on plant diversity, but only at the early successional stages. However, we only found significant effects at one early succession stage (stage 10), but not stage 1 nor 20. At the earliest stage, we found no effects of small herbivores, possibly due to their low abundance. This was driven by low productivity, coincident with the large area of bare ground, short vegetation, and little clay accumulation at this stage (Table S1). As the succession progressed, nutrients accumulated, and productivity increased (Table S1). Likewise, the abundance of herbivores increased at early successional stages (Figure 1). Therefore, effects of small herbivores on plant diversity became apparent. However, we only found significant effects at stage 10. No effects of small herbivores at stage 20 in the short term may due to lack of effects of small herbivores on the dominant grass *F. rubra*. This may be because higher nitrogen availability at stage 20 (clay thickness in 2001 at stage 10:5.93 ± 1.19 (cm); stage 20:12.88 ± 1.09; mean ± 1 se (cm); Table S1) facilitated the regrowth of *F. rubra* even after being heavily grazed (Van Der Graaf, Stahl, & Bakker, 2005; Kuijper, Dubbeld, & Bakker, 2005). Lack of the effects in the long term at stage 20 may be due to the rapid expansion of *E. atherica* in this area in 2016. As Kuijper and Bakker (2005) showed that the presence of *E. atherica* patches, even if they are not very dense, can substantially discourage hare and goose grazing. Similarly, no effects of small herbivores at intermediate and late successional stages in the short and long term were mainly due to the dominance of less preferred *E. atherica*.

Although effects of hares and geese on plant diversity were only significant at one early successional stage, these effects persisted up to 22 years. In addition, hares and geese strongly controlled *F. rubra* and *E. atherica* in the long term. One explanation for this persistence may be that 7 years is already long term. Indeed, some researchers refer to 7 years as long term, and most experiments examining effects of small herbivores on plant diversity in saltmarshes last less than 7 years (Alberti et al., 2011; Bromberg et al., 2009; Daleo et al., 2014; Gough & Grace, 1998a, 1998b; Pascual et al., 2017). However, in this system, 7 years was not long enough to capture the important changes, as the late successional species *E. atherica* did not establish

in any grazing treatment at earlier successional stages (percent cover <2%; including stage 1, 10 and 20) 7 years after the start of the experiment. Additionally, the pattern of plant diversity (except for the earliest stage) 7 years after the start of the experiment was similar to that of 3 years after. However, it was substantially different from that of 22 years after the start of the experiment (Figure S4). Our results suggest that evaluating short and long-term effects of herbivores should also take into account the development and characteristics of the system. More importantly, our results indicate that small herbivores can have a long-lasting impact on plant communities.

Hares and geese together had a larger long-term impact than hares alone on plant communities. In the long term, hares and geese controlled *E. atherica* and *F. rubra* significantly better than hares alone. They also significantly slowed down species loss compared with hares alone at stage 20 in 2016. This is contrary to the previous study showing that hares play a more important role in structuring plant communities in this system based on the 7-year herbivore exclusion experiment (Kuijper & Bakker, 2005). Our long-term experiment indicates that effects of geese could be underestimated in this saltmarsh based on short-term results. Our results also provide clear evidence that herbivores grazing on the same forage plants do have an additive interaction (Ritchie & Olff, 1999), and this became more pronounced in the long term.

Small herbivores slowed down plant diversity decline via decreasing dominance, in accordance with Koerner et al. (2018). However, the dominant species changed in the short and long term. Small herbivores suppressed *F. rubra* in the short term, but *E. atherica* in the long term. In addition, via suppressing *E. atherica*, small herbivores indirectly promoted *F. rubra* in the long term at early successional stages. The dense stands of *F. rubra*, once formed, can in turn substantially resist colonization and establishment of *E. atherica* (Kuijper et al., 2005). This would slow down vegetation succession to the less preferred *E. atherica* (Kuijper & Bakker, 2005), which otherwise speeds up plant diversity decline.

Our long-term herbivore exclusion experiment suggests that small herbivores have an impact on plant diversity in the saltmarsh, but this impact was restricted to the early successional stage. A recent meta-analysis (He & Silliman, 2016) found inconsistent effects of small herbivores on plant diversity in saltmarshes. Our results indicate that one important reason may be that there is a low abundance of small herbivores, driven by low quality and abundance of forage plants. For instance, saltmarshes in North and South America are usually dominated by one or a few tall but not very palatable plant species (Conde et al., 2006; Pennings, Siska, & Bertness, 2001). In such situations, it is not surprising that herbivores do not have an impact on plant diversity (He & Silliman, 2016). In addition, by excluding hares and geese in a hierarchical design, we showed that a more diverse herbivore community has stronger regulating effects on plant communities, especially in the long term. However, more studies are needed to generalize this conclusion over different systems. Rapid expansion of less preferred plant species would drive the decline of small herbivore populations, while predation would exacerbate this decline. The decline in small herbivore populations could in turn affect plant diversity, underlining the importance of conserving small herbivores.

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## AUTHORS' CONTRIBUTIONS

J.P.B. initiated this experiment, and assisted in data collecting. D.P.J.K. counted droppings in 2000 and recorded plant species occurrence and abundance in 2001, while Q.C. did those in 2016. Q.C., R.A.H., J.A., H.O. and C.S. discussed and set the conceptual framework of this manuscript. Q.C. analysed the data and wrote the manuscript. All authors contributed to the revisions and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.kr6409q (Chen et al., 2019).

## ORCID

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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